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REVIEW

Progress and problems in the assessment of flower morphology in higher-level systematics

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Abstract Floral features used for characterization of higher-level angiosperm taxa (families, orders, and above) are assessed following a comparison of earlier (precladistic/premolecular) and current classifications. Cronquist (An integrated system of classification of flowering plants. Columbia University Press, New York, 1981) and APG (Angiosperm Phylogeny Group) (Bot J Linn Soc 161:105–121, 2009) were mainly used as the basis for this comparison. Although current circumscriptions of taxonomic groups (clades) are largely based on molecular markers, it is also important to morphologically characterize these new groups, as, in many cases, they are completely novel assemblages, especially at the level of orders and above. Features used in precladistic/premolecular classifications are often much more evolutionarily plastic than earlier assumed. A number of earlier neglected but potentially useful features at higher levels are discussed based on our own and other recent studies. As certain features tend to evolve repeatedly in a clade, it appears that apomorphic features in the strict sense are less helpful to characterize larger clades than earlier assumed, and rather apomorphic *tendencies* of features are more useful at this level.

Keywords Androecium · Angiosperms · Apomorphic tendencies · Flower morphology · Gynoecium · Higher classification · Orders · Ovules · Perianth

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Introduction

Plant species, genera, families, orders, and even higher categories have long been characterized by structural features, mainly by floral morphology. Certain features have generally been regarded as of special value to characterize higher-level taxa (families and above) in traditional classifications, with the assumption that they are relatively stable. Earlier, classifications were developed whereby larger primary groups were formed based upon shared structural similarity. These groups then constituted the nuclei around which other groups were assembled by concatenation according to their least dissimilarity. By this tentative association of similar groups, "islands" were created that were relatively parsimonious but did not necessarily represent "natural" groups (i.e., groups of related components but not defined whether monophyletic or paraphyletic). Earlier errors in macrosystematics may have been caused by a bias to use central European herbaceous plants as textbook examples for illustration. Floral morphology and systematics would probably have had a different history had they started in South America, Africa, or Australia, instead of Europe.

In the premolecular era certain floral features were regarded as primitive and others as advanced at a global level in angiosperms. Such features were, for instance, large versus small number of floral organs, spiral versus whorled floral phyllotaxis, free versus united petals, free versus united carpels, and superior versus inferior ovary. However, this somewhat simplistic and vague view on flower evolution has been challenged by the impressive new insights provided by molecular phylogenetic studies over the past 20 years, beginning forcibly with the groundbreaking comparative molecular study on 500 seed plant taxa by Chase et al. (1993) and further advanced by

many authors since (e.g., Soltis et al. 2011). We now have a much better picture of relationships between families and orders than 20 years ago (Fig. 1). This is important to emphasize, even if many new higher-level relationships are not yet well supported and substantial changes are still to be expected. Specifically, the APG (Angiosperm Phylogeny Group) classifications (most recently APG 2009; see also Stevens 2001 onward) review the current state of relationships in a concise way and reflect the profound changes and (to some extent) the relationships that are still uncertain. The continuing refinement in these phylogenetic studies with more taxa and more nucleotides studied further sharpens this picture at all levels of the systematic hierarchy. As a consequence, various problems of flower morphology need to be tackled in a new way. The aim of this review is therefore an assessment of the floral features used in characterization of higher taxonomic groups before the molecular revolution and now. The work by Cronquist (1981) is used for comparison because the average size of his orders (83 orders, 383 families) and families is comparable to that in APG (2009) (63 orders, 415 families) and is therefore convenient for comparison, whereas it is smaller in the pre-APG [APG (angiosperm phylogeny group) 1998] classifications by Takhtajan (1987, 1997) and larger in those by Thorne (1983, 1992), and also because Cronquist (1981) describes his groups in more detail than the other authors. We should emphasize that the newly recognized clades in molecular phylogenetic analyses are in most cases morphologically unstudied and thus black boxes. A large effort is necessary to remedy this situation (Crane et al. 2004; Endress and Friis 2006; Endress and Matthews 2006b; Schönenberger and von Balthazar 2006). Thus, what does a comparison of old and new classifications tell us about our earlier mistakes in the systematic evaluation of floral structure? Because flower structure (incl. embryology) was a primary basis for the building of earlier classifications, it is useful to focus on flowers for such a comparison. Even in the molecular era, comparative morphological analyses are used for tree building, often in combination with molecular studies. Such combined studies may give better resolution of the trees (e.g., Nandi et al. 1998; Doyle and Endress 2000). Morphological analyses are also important for the placement of fossils (e.g., Endress and Doyle 2009; Doyle and Endress 2010) and become even more important as more fossils become available (Friis et al. 2011). They may also be helpful in resolving uncertain topologies, such as those of a number of rosid orders and the relationship between fabids and malvids (Endress and Matthews 2006b; Qiu et al. 2010).

Several topics are addressed in this review: (1) Stability: in spite of the revolution in angiosperm classification, not everything has changed. A few larger groupings that have remained unchanged are shown; (2) Former circumscriptions with considerable changes: a number of premolecular groups (mainly orders, mainly from Cronquist 1981) that have been greatly disassembled are selected to show how their flowers were formerly used for group characterization. Orders with massive changes occur, especially in the basal angiosperms and in rosids, whereas asterids and monocots are less affected. We explore which floral features may have been used to hold them together at that time; (3) Groups with new circumscriptions: a number of new groups (mainly orders) that are completely new or have been greatly reassembled are selected to show first results on their floral morphological characterization. Such clades newly established by molecular phylogenetic studies are largely unknown in their structure and biology; (4) Floral features used to characterize former groups of the premolecular/precladistic era: these may serve to show why morphologists were misled in the composition and characterization of clades in this era; (5) Floral features of new groups: some floral features that have been identified as interesting at the new family or order level are discussed, mainly resulting from comparative studies in orders of rosids by our laboratory and other colleagues; (6) Floral features to be further explored: a number of potentially interesting features have been identified that need to be explored in a wider range of families, orders, and supraordinal groups.

Stability in the classification

Despite the great revolution in our understanding of higher-level angiosperm clades, not everything at this level has changed since the premolecular era. Such stability reflects the sound use of morphological criteria in the premolecular era for the groups where this stability occurs. Some orders of several families (of Cronquist 1981) have not changed in their circumscription, such as Zingiberales and Santalales (in Santalales two families that were already doubtful to Cronquist were removed). In Zingiberales, in addition, even the family circumscriptions did not change (Bartlett and Specht 2010).

In Santalales, however, there are changes in the family circumscriptions (Nickrent et al. 2010). Here the phylogenetic topology prompted recognition of additional families in order to have monophyletic units. The former Olacaceae and Santalaceae were split into several new families: the Olacaceae to avoid paraphyletic groups, and the Santalaceae in order to keep the nested Viscaceae as a family (Malécot and Nickrent 2008; Nickrent et al. 2010).

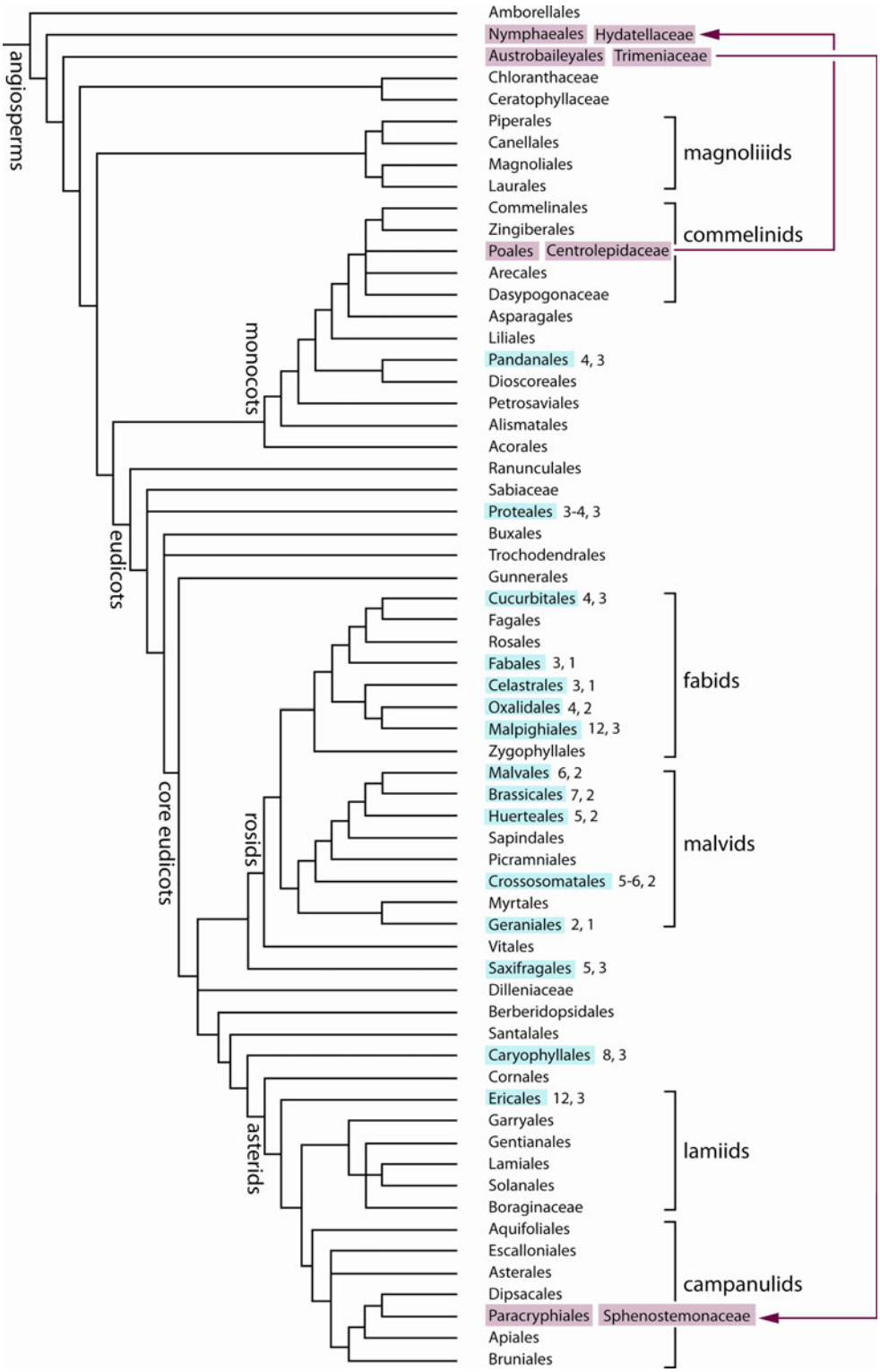

Fig. 1 Cladogram of angiosperm orders from APG (Angiosperm Phylogeny Group) (2009), modified. Highlighted in *blue* are those orders discussed in the text that have undergone considerable changes in their circumscription. The numbers after each name represent the number of orders and subclasses from Cronquist (1981) in which the families of the new order were placed. Highlighted in *red* are the two examples of families discussed in the text that have undergone an extreme change in their position

As a result the order now contains 18 families (Nickrent et al. 2010) versus 8 in Cronquist (1981), not counting the two doubtful families.

Another case of relative stability are Scrophulariales, in which the members of all 12 earlier families are still included, but the order (now named Lamiales) has become enlarged by the addition of families from other earlier orders (Lamiales, Callitrichales, and Plantaginales), in addition to changes in family circumscriptions (Tank et al. 2006; APG 2009)

Former circumscriptions with considerable changes

Former subclasses

Three of the 11 subclasses of Cronquist (1981) were dismantled and the components relegated to other subclasses as a consequence of molecular phylogenetics.

Arecidae (Arecales, Cyclanthales, Pandanales, and Arales) are now positioned in Alismatales, Pandanales, commelinids (APG 2009). They were superficially united by the presence of numerous small, inconspicuous flowers in spikes or spadices. Molecular phylogenetic studies identified these orders as not forming a clade, except for Cyclanthales and Pandanales (Chase et al. 1993, and later works).

Dilleniidae (Dilleniales, Theales, Malvales, Lecythidales, Nepenthales, Violales, Salicales, Capparales, Batales, Ericales, Diapensiales, Ebenales, and Primulales) are now positioned in many different rosids and asterids and some incertae sedis. Dilleniidae were conceived as a major group of dicots by Cronquist (1957, there called Dilleniales) and Takhtajan (1964). This was mainly based on the discovery of centrifugal stamen initiation in a number of mainly large-flowered dicot families by Corner (1946) (Fig. 2a–f). However, molecular phylogenetic analyses showed that these centrifugal groups do not form a clade (Chase et al. 1993, and later works; see also below).

Hamamelididae (Trochodendrales, Hamamelidales, Daphniphyllales, Didymelales, Eucommiales, Urticales, Leitneriales, Juglandales, Myricales, Fagales, and Casuarinales) are now mainly positioned in Saxifragales and Fagales, some also in Rosales, Sapindales, in basal eudicots (Trochodendrales, Buxales) and asterids (Garryales). Hamamelididae were recognized by Takhtajan (1964) as a subclass (Cronquist 1981, used the incorrect spelling "Hamamelidae"). Earlier they were called Amentiferae (Takhtajan 1959). This grouping goes back to Hallier (1896), based on often small, apetalous, unisexual flowers in dense spikes or thyrses ("catkins"). In the 1960s there was still debate about whether angiosperms were monophyletic or polyphyletic (diphyletic), with the adherents of polyphyly (diphyly) tending to believe that a fundamental split existed between stachyosporous and phyllosporous groups of angiosperms, although no critical comparative study had ever been made between them (discussion in Endress 1967).

To critically study this issue, Endress (1967) compared two families, one of each group: Hamamelidaceae (believed to be phyllosporous) and Betulaceae (believed to be stachyosporous by some authors). The result was great congruence, and no fundamental difference in gynoecium structure. This lack of a fundamental split was later confirmed in molecular phylogenetic studies. Great further similarities in floral and vegetative structures prompted Endress (1967, 1977) to assume even close relationships between the two families, in support of earlier ideas by Hallier (1896) and Takhtajan (1959). This, however, was later shown to be erroneous by molecular phylogenetic studies (Chase et al. 1993; Manos and Steele 1997; Qiu et al. 1998; Wang et al. 2009) and Cretaceous flowers of Fagales (Friis et al. 2006). This was also already anticipated by Walker and Doyle (1975) and Wolfe et al. (1975) because of the much more derived pollen in Fagales (derived from tricolporate rather than tricolpate forms as in

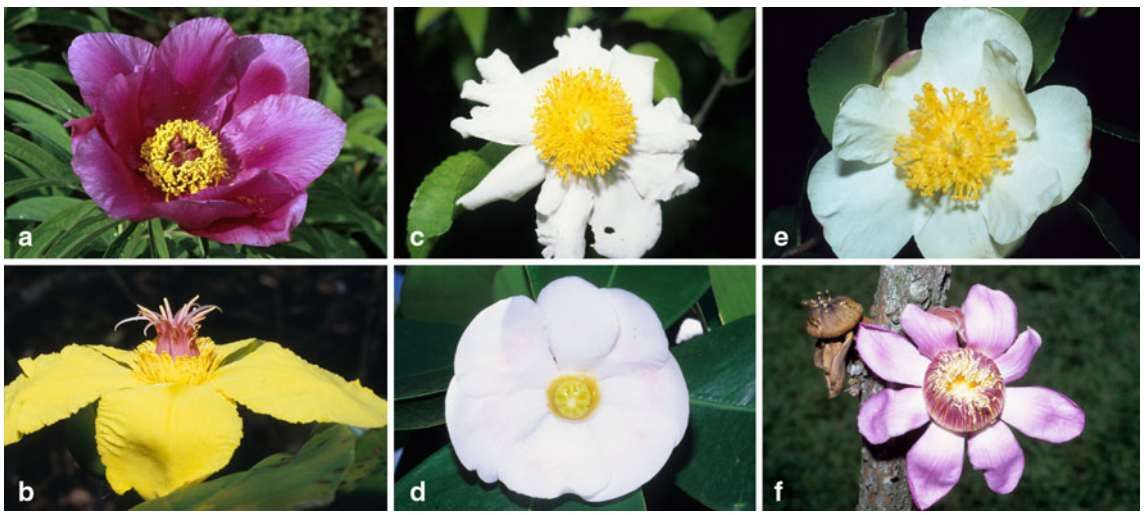

Fig. 2 Large polystemonous flowers in different core eudicot orders (earlier all in Dilleniidae). **a** *Paeonia officinalis* L. (Paeoniaceae, Saxifragales, basal core eudicots). **b** *Dillenia alata* (R. Br. ex DC.) Banks ex Martelli (Dilleniaceae, Dilleniales, basal core eudicots). **c** *Oncoba spinosa* Forssk. (Achariaceae, Malpighiales, rosids). **d** *Clusia rosea* Jacq. (Clusiaceae, Malpighiales, rosids). **e** *Camellia sasanqua* Thunb. (Theaceae, Ericales, asterids). **f** *Gustavia gracillima* Miers (Lecythidaceae, Ericales, asterids)

Hamamelidaceae). The current position of Hamamelidaceae and Betulaceae is in the rosid alliance (name used in Endress 2010a) or Superrosidae (name used in Soltis et al. 2011) but at different positions in this group: the former in Saxifragales and the latter in Fagales (APG 2009). In addition, a few families of Cronquist's (1981) Hamamelid(id)ae are now positioned in basal eudicots; these have largely dimerous flowers and a poorly differentiated perianth or no perianth at all (*Didymeles* of Didymelaceae; von Balthazar et al. 2003; *Tetracentron* of Trochodendraceae; Endress 1986; Chen et al. 2007).

Former orders

Out of the 83 orders in Cronquist (1981), 18 that underwent considerable changes in their composition are selected here to show which floral features were used earlier for characterization and where their components were transferred following molecular phylogenetic results.

Magnoliales (Winteraceae, Degeneriaceae, Himantandraceae, Eupomatiaceae, Austrobaileyaceae, Annonaceae, Magnoliaceae, Lactoridaceae, Myristicaceae, and Canellaceae) in Magnoliidae. These families are now in Canellales, Magnoliales, Austrobaileyales, and Piperales, dispersed in the ANITA grade and magnoliids. Old unifying features: flowers mostly large, often with trimerous whorls or spiral, apocarpous, carpels with several or numerous lateral ovules.

Laurales (Amborellaceae, Trimeniaceae, Monimiaceae, Gomortegaceae, Calycanthaceae, Idiospermaceae, Lauraceae, and Hernandiaceae) in Magnoliidae. These families are now in Amborellales, Austrobaileyales, and Laurales, dispersed in the ANITA grade and magnoliids. Old unifying features: flowers often with trimerous whorls or spiral, often with floral cup, apocarpous, carpels with a single median ovule (in Calycanthaceae two lateral ovules).

Nymphaeales (Nelumbonaceae, Nymphaeaceae, Barclayaceae, Cabombaceae, and Ceratophyllaceae) in Magnoliidae. These families are now in Proteales, Nymphaeales, and Ceratophyllales, dispersed in the ANITA grade, basal eudicots, and of unknown position. Old unifying features: water plants, polystemonous, apocarpous (except for Nymphaeaceae, Barclayaceae).

Liliales (Philydraceae, Pontederiaceae, Haemodoraceae, Cyanastraceae, Liliaceae, Iridaceae, Velloziaceae, Aloeaceae, Agavaceae, Xanthorrhoeaceae, Hanguanaceae, Taccaceae, Stemonaceae, Smilacaceae, and Dioscoreaceae) in Liliidae. These families are now in Commelinales, Liliales, Asparagales, Pandanales, and Dioscoreales, all in monocots. Old unifying features: flowers trimerous, outer and inner perianth organs similar, diplostemonous.

Hamamelidales (Cercidiphyllaceae, Eupteleaceae, Platanaceae, Hamamelidaceae, and Myrothamnaceae) in Hamamelid(id)ae. These families are now in Ranunculales, Proteales, and Gunnerales (basal eudicots), and Saxifragales (core eudicots). Old unifying features: early flowering, wind-pollinated, perianth inconspicuous or lacking, stamens basifixed, anthers with valves, connective protrusion, pollen tricolpate, long, free style, large stigma.

Dilleniales (Dilleniaceae and Paeoniaceae) in Dilleniidae. These families are now in Dilleniales and Saxifragales, both in basal core eudicots. Old unifying features: flowers large, outer floral phyllotaxis spiral, polystemony, centrifugal stamen initiation (Corner 1946), apocarpous.

Theales (Caryocaraceae, Ochnaceae, Sphaerosepalaceae, Sarcolaenaceae, Dipterocarpaceae, Theaceae, Actinidiaceae, Scytopetalaceae, Tetrameristaceae, Pellicieraceae, Oncothecaceae, Marcgraviaceae, Quiinaceae, Elatinaceae, Paracryphiaceae, Medusagynaceae, and Clusiaceae) in Dilleniidae. These families are now in Malpighiales, Malvales, Ericales, and Paracryphiales, or not yet placed, dispersed in rosids and asterids. Old unifying features: flowers ± large, often polystemonous, placenta axile (plus concatenation of families with partly similar features).

Violales (Flacourtiaceae, Peridiscaceae, Bixaceae, Cistaceae, Huaceae, Lacistemataceae, Scyphostegiaceae, Stachyuraceae, Violaceae, Tamaricaceae, Frankeniaceae, Dioncophyllaceae, Ancistrocladaceae, Turneraceae, Malesherbiaceae, Passifloraceae, Achariaceae, Caricaceae, Fouquieriaceae, Hoplestigmataceae, Cucurbitaceae, Datiscaceae, Begoniaceae, and Loasaceae) in Dilleniidae. These families are now in as many as 11 orders: Malpighiales, Saxifragales, Malvales, Oxalidales, Crossosomatales, Caryophyllales, Brassicales, Ericales, Boraginales (Hoplestigmataceae), Cucurbitales, and Cornales, dispersed in rosids and asterids (incl. Caryophyllales). Old unifying features: gynoecium often trimerous, placentae often parietal (plus concatenation of families with partly similar features).

Rosales (Brunelliaceae, Connaraceae, Eucryphiaceae, Cunoniaceae, Dialypetalanthaceae, Pittosporaceae, Byblidaceae, Hydrangeaceae, Columelliaceae, Grossulariaceae, Greyiaceae, Bruniaceae, Alseuosmiaceae, Crassulaceae, Cephalotaceae, Saxifragaceae, Davidsoniaceae, Anisophylleaceae, Crossosomataceae, Rosaceae, Neuradaceae, Chrysobalanaceae, Surianaceae, and Rhabdodendraceae) in Rosidae. These families are now in as many as 15 orders: Oxalidales, Gentianales, Apiales, Ericales, Cornales, Bruniales, Saxifragales, Geraniales, Asterales, Cucurbitales, Crossosomatales, Rosales, Malvales, Malpighiales, and Fabales, dispersed in rosids and asterids and in Saxifragales and Caryophyllales. Old unifying features: in case of polystemony centripetal stamen initiation, mostly free styles, sometimes apocarpy (many with apocarpy placed here: Brunelliaceae, Connaraceae, Crassulaceae, Cephalotaceae, Crossosomataceae, Rosaceae, and Surianaceae) (plus concatenation of families with partly similar

features–almost a rubbish bin of families that are otherwise difficult to place).

Rafflesiales (Hydnoraceae, Mitrastemonaceae, and Rafflesiaceae) in Rosidae. These families are now in Piperales, Ericales, Malpighiales, and additional families (such as Cytinaceae and Apodanthaceae that were part of Cronquist's Rafflesiaceae) in Malvales, and Cucurbitales (?), dispersed in magnoliids, rosids, and asterids. Old unifying features: parasites with mycelium-like or massive haustoria, androecium often without thecal organization.

Celastrales (Geissolomataceae, Celastraceae, Hippocrateaceae, Stackhousiaceae, Salvadoraceae, Aquifoliaceae, Icacinaceae, Aextoxicaceae, Cardiopteridaceae, Corynocarpaceae, and Dichapetalaceae) in Rosidae. These families are now in Crossosomatales, Celastrales, Brassicales, Aquifoliales, Berberidopsidales, Cucurbitales, and unplaced in lamiids, dispersed in rosids and asterids, and Berberidopsidales. Old unifying features: flowers small, haplostemonous, stamens antesepalous.

Euphorbiales (Buxaceae, Simmondsiaceae, Pandaceae, and Euphorbiaceae) in Rosidae. These families are now in Buxales, Caryophyllales, Malpighiales, dispersed in basal eudicots, Caryophyllales, and rosids. Old unifying features: flowers unisexual, petals mostly lacking, gynoecium and often also outer floral whorls trimerous, fruits cocci or capsules. This is a very mixed bag of rosids, Caryophyllales, and basal eudicots. Trimerous gynoecia or flowers are derived from several different origins. Buxaceae are primitively dimerous, and trimery, in the few genera where it occurs, is derived (von Balthazar and Endress 2002a, b; von Balthazar et al. 2000). In Euphorbiaceae and Pandaceae it is most probably derived from pentamery (Wurdack and Davis 2009).

Polygalales (Malpighiaceae, Vochysiaceae, Trigoniaceae, Tremandraceae, Polygalaceae, Xanthophyllaceae, and Krameriaceae) in Rosidae. These families are now in Malpighiales, Myrtales, Oxalidales, Fabales, and Zygophyllales, all in rosids. Old unifying features: flowers mostly monosymmetric, gynoecium tri- or dimerous.

Sapindales (Zygophyllaceae, Staphyleaceae, Melianthacae, Bretschneideraceae, Akaniaceae, Sapindaceae, Hippocastanaceae, Aceraceae, Burseraceae, Anacardiaceae, Julianiaceae, Simaroubaceae, Cneoraceae, Meliaceae, and Rutaceae) in Rosidae. These families are now in Zygophyllales, Crossosomatales, Geraniales, Brassicales, and Sapindales, all in rosids. Old unifying features: flowers often obliquely monosymmetric, flowers (ob)diplostemonous, gynoecium pentamerous or trimerous.

Malvales (Elaeocarpaceae, Tiliaceae, Sterculiaceae, Bombacaceae, and Malvaceae) in Dilleniidae. These families are now in Oxalidales and Malvales, both in rosids. Old unifying features: flowers often large, sepals valvate, petals contort, polystemonous, gynoecium pentamerous.

Geraniales (Oxalidaceae, Geraniaceae, Limnanthaceae, Tropaeolaceae, and Balsaminaceae) in Rosidae. These families are now in Oxalidales, Geraniales, Brassicales, and Ericales, dispersed in rosids and asterids. Old unifying features: flowers often isomerous (ob)diplostemonous, gynoecium mostly pentamerous.

Solanales (Duckeodendraceae, Nolanaceae, Solanaceae, Convolvulaceae, Menyanthaceae, Polemoniaceae, and Hydrophyllaceae) in Asteridae. These families are now in Solanales, Asterales, Ericales, and Boraginales, all in asterids (basal asterids, lamiids, and campanulids). Old unifying features: flowers mostly polysymmetric, sympetalous, carpels with numerous ovules.

Lamiales (Lennoaceae, Boraginaceae, Verbenaceae, and Lamiaceae) in Asteridae. These families are now in Boraginales and Lamiales, both in lamiids. Old unifying features: carpels with two ovules, ovaries with false septum, each part bulging, giving rise to mostly four schizocarps.

Former families

Three of the families that underwent extreme changes are addressed here: Scrophulariaceae and Icacinaceae in Cronquist's (1981) circumscription, and Saxifragaceae in Engler's (1930) circumscription.

Scrophulariaceae are now in ca. seven families, all in Lamiales [Scrophulariaceae, Plantaginaceae, Orobanchaceae, Calceolariaceae, Linderniaceae, Phrymaceae, Rehmanniaceae (Reveal 2011; *Rehmannia* not mentioned in Cronquist 1981, but in Takhtajan 1997, in Scrophulariaceae)]. The old Scrophulariaceae were characterized by: flowers monosymmetric, perianth 5-merous, four stamens, two carpels, fruit capsules with several to numerous seeds.

Icacinaceae are now in four families and in two (or perhaps three?) orders of asterids and there in lamiids and campanulids (Karehed 2001): Metteniusaceae are placed in Metteniusales (Reveal and Chase 2011, or, unplaced to order, in lamiids, APG 2009; see also González et al. 2007; González and Rudall 2010). Icacinaceae are placed in Icacinales (Reveal and Chase 2011, or, unplaced to order, in lamiids, APG 2009). Stemonuraceae and Cardiopteridaceae are placed in Aquifoliales, in campanulids (APG 2009). The old Icacinaceae were characterized by: flowers small, 4–5-merous, petals valvate, stamens antesepalous, filaments often hairy near the tip, mostly three carpels, usually functionally unilocular, ovules (1)–2, pendant, unitegmic, crassinucellar to tenuinucellar.

One of the most extreme examples of dismantled families are Engler's (1930) *Saxifragaceae*, although Cronquist (1981) had already somewhat improved their classification (see also Wagenitz 1997). Their components are now placed in 20 families and 12 orders (Saxifragales, Geraniales, Celastrales, Crossosomatales, Myrtales, Oxalidales,

Cornales, Aquifoliales, Solanales, Escalloniales, Paracryphiales, and Asterales), in basal core eudicots, rosids (both fabids and malvids), and in asterids (both lamiids and campanulids). Engler's Saxifragaceae show a simple type of flowers of moderate synorganization: 5-merous, choripetalous, diplostemonous or haplostemonous, two carpels, more or less united, numerous ovules.

Groups with new circumscriptions

New orders or previous orders with fundamental reorganization

Of interest are also completely newly established orders of several families or previous orders with extensive reorganization. Fifteen such orders as recognized in APG (2009) are selected to be addressed here (Fig. 1).

Pandanales (Pandanaceae, Cyclanthaceae, Stemonaceae, Triuridaceae, and Velloziaceae; Chase et al. 2000). Earlier Pandanales consisted only of Pandanaceae. The current five families were in four earlier orders (Pandanales, Cyclanthales, Liliales, and Triuridales), of three subclasses (Arecidae, Liliidae, and Alismatidae). Floral merism is labile in contrast to most other monocot groups, and there are trends to polystemonous flowers in four of the five families, and to dimerous flowers in two families (Rudall and Bateman 2006).

Proteales (Proteaceae, Platanaceae, Nelumbonaceae, and perhaps also Sabiaceae; Chase et al. 1993). Proteales are a completely new order. The current three or four families were in three or four different earlier orders (Proteales, Hamamelidales, Nymphaeales, and Ranunculales), of three subclasses (Rosidae, Hamamelididae, and Magnoliidae). Flowers show almost no syncarpy, di- or trimery in perianth and androecium (not in Nelumbonaceae), and show a trend to orthotropous ovules (not in Nelumbonaceae) (Endress and Igersheim 1999; von Balthazar and Schönenberger 2009). This is one of the most puzzling new assemblages. It is an ancient group. Platanaceae were very diverse in the lower Cretaceous (Friis et al. 1988; Crane et al. 1993; Magallón et al. 1997), but only one genus is left today. The giant flowers of *Nelumbo* are derived as suggested by the much smaller lower Cretaceous fossil *Nelumbites* (Upchurch et al. 1994; Doyle and Endress 2010). This high divergence is believed to be due to early adaptation to very different habitats. There is some coherence in the floral organization of Proteaceae, Sabiaceae, and Platanaceae, but Nelumbonaceae have diverged greatly from the ancestral structure concomitant with the advent of floral gigantism. A similar divergence is present in Nymphaeales with the giant flowers of Nymphaeaceae in contrast to the much smaller flowers of Cabombaceae and Hydatellaceae (Davis et al. 2008).

Saxifragales (Altingiaceae, Aphanopetalaceae, Cercidiphyllaceae, Crassulaceae, Daphniphyllaceae, Grossulariaceae, Haloragaceae, Hamamelidaceae, Iteaceae, Pterostemonaceae, Paeoniaceae, Penthoraceae, Peridiscaceae, Saxifragaceae, and Tetracarpaeaceae; Jian et al. 2008). Saxifragaceae were earlier in Rosales, together with 23 other families, among them only 2 other families now in Saxifragales; the current 15 families of Saxifragales were in five earlier orders (Hamamelidales, Daphniphyllales, Dilleniales, Rosales, and Haloragales), of three subclasses (Hamamelididae, Dilleniidae, and Rosidae). Flowers have basifixed or centrifixed anthers, a bicarpellate gynoecium or the flowers are isomerous in all organ categories; there is a tendency to apocarpy or at least free styles, often also free upper part of ovary (Endress 1989b; Endress and Stumpf 1991; Magallón 2007).

Fabales (Fabaceae, Polygalaceae, Surianaceae, and Quillajaceae; Bello et al. 2009). This is a completely new assemblage of families. The current four families were in three earlier orders (Fabales, Polygalales, and Rosales), all from subclass Rosidae. There is a tendency towards monosymmetric and in some cases even pronouncedly asymmetric flowers (keel flowers), and a tendency of dorsally upwards-bulging ovaries (Bello et al. 2007, 2010).

Cucurbitales (Anisophylleaceae, Coriariaceae, Corynocarpaceae, Cucurbitaceae, Begoniaceae, Datiscaceae, and Tetramelaceae; Zhang et al. 2006; uncertain: Apodanthaceae; Filipowicz and Renner 2010; Schaefer and Renner 2011). This is a largely new assemblage of families. Cucurbitaceae, with Datiscaceae and Begoniaceae, were earlier in Violales (Cronquist 1981). The current seven families were in four earlier orders (Violales, Ranunculales, Rosales, and Celastrales), of three subclasses (Magnoliidae, Dilleniidae, and Rosidae). There is a tendency to unisexual, nectarless flowers; sepals and petals are often similar, both pointed (Matthews and Endress 2004); Coriariaceae were misinterpreted by Cronquist (1981) as apocarpous. They are clearly syncarpous with a normal compitum (Matthews and Endress 2004).

Oxalidales (Oxalidaceae, Connaraceae, Brunelliaceae, Cephalotaceae, Cunoniaceae, Elaeocarpaceae, and Tremandraceae; Savolainen et al. 2000). The current seven families were in four earlier orders (Geraniales, Rosales, Malvales, and Polygalales), of two subclasses (Dilleniidae and Rosidae). The flowers show a tendency to (ob)diplostemony and isomery and a tendency to apocarpy or at least free styles; ovules often have an endothelium, even if crassinucellar, and a medianly directed slit-like micropyle (Matthews and Endress 2002).

Celastrales (Celastraceae, Parnassiaceae, and Lepidobotryaceae; Zhang and Simmons 2006). The current three

families were in three earlier orders (Celastrales, Rosales, and Geraniales), all of subclass Rosidae. Petals are not retarded in development and form protective organs in bud. Stamens are united with ovaries; gynoecia have locules that are dorsally bulged upward combined with apical septa, and commissural stigmas associated with strong commissural vascular bundles (not in Lepidobotryaceae); the carpel ventral slits are closed by long interlocking epidermal cells and have conspicuous pollen tube transmitting tracts encompassing several cell layers; they have only weakly crassinucellar or incompletely tenuinucellar ovules with an endothelium (crassinucellar without endothelium in Lepidobotryaceae) (Matthews and Endress 2005a).

Malpighiales (Achariaceae, Balanopaceae, Bonnetiaceae, Calophyllaceae, Caryocaraceae, Centroplacaceae, Chrysobalanaceae, Clusiaceae, Ctenolophonaceae, Dichapetalaceae, Elatinaceae, Erythroxylaceae, Euphorbiaceae, Euphroniaceae, Goupiaceae, Humiriaceae, Hypericaceae, Irvingiaceae, Ixonanthaceae, Lacistemaceae, Linaceae, Lophopyxidaceae, Malesherbiaceae, Malpighiaceae, Ochnaceae, Medusagynaceae, Quiinaceae, Pandaceae, Passifloraceae, Peraceae, Phyllanthaceae, Picrodendraceae, Podostemaceae, Putranjivaceae, Rafflesiaceae, Rhizophoraceae, Salicaceae, Trigoniaceae, Turneraceae, and Violaceae; Wurdack and Davis 2009; Ruhfel et al. 2011). This is a new order with many components that were earlier regarded as unrelated. The current 40 families (as in Wurdack and Davis 2009) were in 12 earlier orders (Fagales, Violales, Theales, Rosales, Linales, Celastrales, Euphorbiales, Polygalales, Sapindales, Podostemales, Rafflesiales, and Rhizophorales), of three subclasses (Hamamelididae, Dilleniidae, and Rosidae); *Centroplacus* is not mentioned in Cronquist (1981); in Takhtajan (1997) it is in Pandaceae of his Euphorbiales. There is a tendency to antitropous ovules with an obturator, and ovules are often weakly crassinucellar or incompletely tenuinucellar, often with an endothelium (Merino Suter et al. 2006; Matthews and Endress 2008, 2011).

Geraniales (Geraniaceae, Vivianiaceae, and Melianthaceae; Soltis et al. 2000). The three current families were in two earlier orders (Geraniales and Sapindales), both in Rosidae. Flowers are (ob)diplostemonous and completely isomerous; the carpels are conspicuously bulged outwards in the ovary (Sauer 1933; Ronse Decraene and Smets 1999a; Ronse Decraene et al. 2001).

Crossosomatales (Crossosomataceae, Stachyuraceae, Staphyleaceae, Guamatelaceae, Aphloiaceae, Geissolomataceae, Ixerbaceae, and Strasburgeriaceae; Cameron 2003; Sosa and Chase 2003). This is a completely new order (Reveal 1993), including the recently acquired new family, Guamatelaceae (*Guamatela*, earlier in Rosaceae) (Oh and Potter 2006). The current eight families were in five or six earlier orders (Violales, Theales, Rosales, Sapindales, and Celastrales), of two subclasses (Dilleniidae and Rosidae); *Ixerba* is not mentioned in Cronquist (1981); it is close to *Brexia* (Celastranae) in Takhtajan (1997). Flowers show a tendency towards apocarpy but concomitantly postgenital union of carpels; pollen buds are prominent (Matthews and Endress 2005b).

Huerteales (Dipentodontaceae, Tapisciaceae, Gerrardinaceae, and Petenaeaceae; Worberg et al. 2009). This is a completely new order (Doweld 2001) with two new families: Gerrardinaceae (Alford 2006) and Petenaeaceae (Christenhusz et al. 2010). The current four families with six genera were in five different earlier orders (Violales, Malvales, Sapindales, Celastrales, and Santalales), of two subclasses (Dilleniidae and Rosidae). One of the families, Dipentodontaceae, even has two genera of two different earlier orders (*Dipentodon* in Santalales in Cronquist 1981, *Perrottetia* not mentioned in Cronquist 1981, but in Celastrales in other classifications; floral morphologically out of place in Celastrales; Matthews and Endress 2005a). Tapisciaceae contain *Tapiscia* and *Huertea* (in Sapindales in Cronquist 1981), Gerrardinaceae contain *Gerrardina* (in Violales in Cronquist 1981), Petenaeaceae contain *Petenaea* (not mentioned by Cronquist 1981, positioned in Malvales by other authors, see Christenhusz et al. 2010). Flowers are poorly studied; they are small, simple, with the carpels completely congenitally united (as far as known).

Brassicales (core families: Brassicaceae, Capparaceae, Cleomaceae, Gyrostemonaceae, Resedaceae, and Tovariaceae; "basal" families: Akaniaceae, Bretschneideraceae, Bataceae, Caricaceae, Emblingiaceae, Koeberliniaceae, Limnanthaceae, Moringaceae, Pentadiplandraceae, Salvadoraceae, Setchellanthaceae, and Tropaeolaceae; Rodman et al. 1996). Most of the "basal" families were newly added to the order. The predominant presence of glucosinolates is further supported. The current 18 families were in seven earlier orders (Sapindales, Batales, Capparales, Violales, Polygalales, Geraniales, and Celastrales), of two subclasses (Dilleniidae and Rosidae); Setchellanthaceae (Iltis 1999; Karol et al. 1999) are a new family segregated from Capparaceae. Commissural stigmas occur in core Brassicales. There is a tendency to campylotropous and incompletely tenuinucellar ovules (Ronse Decraene and Haston 2006).

Malvales [Bixaceae, Cistaceae, Cytinaceae, Dipterocarpaceae, Malvaceae, Muntingiaceae, Neuradaceae, Sarcolaenaceae, Sphaerosepalaceae, and Thymelaeaceae; Bayer et al. 1999; perhaps also Apodanthaceae (Schaefer and Renner 2011; supported by floral structure: Blarer et al. 2004; Endress 2010a)]. The present 10 families were in six earlier orders (Violales, Theales, Malvales, Rafflesiales, Rosales, and Myrtales), of two subclasses (Dilleniidae and Rosidae). There are tendencies towards contort petals, toward polystemony with centrifugal stamen

initiation, either on a primary ring meristem or with primary sectorial meristems, and a slight tendency towards orthotropous ovules (Ronse Decraene 1989; Nandi 1998a, b; von Balthazar et al. 2006).

Caryophyllales (Achatocarpaceae, Aizoaceae, Amaranthaceae, Anacampserotaceae, Ancistrocladaceae, Asteropeiaceae, Barbeuiaceae, Basellaceae, Cactaceae, Caryophyllaceae, Didiereaceae, Dioncophyllaceae, Droseraceae, Drosophyllaceae, Frankeniaceae, Gisekiaceae, Halophytaceae, Limeaceae, Lophiocarpaceae, Molluginaceae, Montiaceae, Nepenthaceae, Nyctaginaceae, Physenaceae, Phytolaccaceae, Plumbaginaceae, Polygonaceae, Portulacaceae, Rhabdodendraceae, Sarcobataceae, Simmondsiaceae, Stegnospermataceae, Talinaceae, and Tamaricaceae; Cuénoud et al. 2002). The core Caryophyllales did not change much in their circumscription since the premolecular time, but Rhabdodendraceae, Simmondsiaceae, Physenaceae, and Asteropeiaceae were added, and six new families were erected: Sarcobataceae (Behnke 1997), Talinaceae (Doweld 2001), Limeaceae (Hoogland and Reveal 2005), Microteaceae (Schäferhoff et al. 2010), Lophiocarpaceae (Doweld and Reveal 2008), and Anacampserotaceae (Nyffeler and Eggli 2010). An additional subclade with 10 families newly assembled together was incorporated into the order (Nepenthaceae, Ancistrocladaceae, Dioncophyllaceae, Droseraceae, Drosophyllaceae, Nepenthaceae, Frankeniaceae, Tamaricaceae, Plumbaginaceae, and Polygonaceae; Albert et al. 1992). The current 34 families are from eight earlier orders (Caryophyllales, Plumbaginales, Polygonales, Violales, Theales, Nepenthales, Rosales, and Euphorbiales; *Physena* not mentioned), of three subclasses (Caryophyllidae, Dilleniidae, and Rosidae). Petals are ancestrally lacking, but evolved in parallel in many families (Brockington et al. 2010); campylotropous ovules are predominant (mainly in the core clade), and ovules with long funicles are conspicuous (Eckardt 1976; Endress 2010a).

Ericales (Balsaminaceae, Tetrameristacae, Fouquieriaceae, Polemoniaceae, Lecythidaceae, Sladeniaceae, Pentaphylacaceae, Sapotaceae, Ebenaceae, Primulaceae, Theaceae, Symplocaceae, Diapensiaceae, Styracaceae, Sarraceniaceae, Roridulaceae, Actinidiaceae, Clethraceae, Cyrillaceae, Mitrastemonaceae, and Ericaceae; Anderberg et al. 2002; Schönenberger et al. 2005). Ericales have been expanded with many new components. The present 21 families were in 12 earlier orders (Ericales, Diapensiales, Ebenales, Primulales, Lecythidales, Theales, Violales, Nepenthales, Geraniales, Rosales, Rafflesiales, and Solanales; *Sladenia* not mentioned), of 3 earlier subclasses (Dilleniideae, Rosidae, and Asteridae). Flowers are mostly sympetalous, haplostemonous or (ob)diplostemonous; ovules have one or two integuments, and are only incompletely tenuinucellar (Schönenberger et al. 2005, 2010).

New family positions with drastic changes

Many families have changed their positions into other orders or supraordinal clades. Two drastic changes are addressed here, involving: (1) transfers from basal angiosperms (ANITA grade) to highly derived core eudicots (asterids), and (2) from highly derived monocots (commelinids) to basal angiosperms (ANITA grade).

1. Paracryphiales (consisting of three unigeneric families, Paracryphiaceae, Sphenostemonaceae, and Quintiniaceae) are now sister to Dipsacales (campanulids, asterids) based on molecular analyses (Tank & Donoghue 2010). *Paracryphia* and *Sphenostemon* were earlier believed to be in families of today's basal angiosperms: The monotypic *Paracryphia* was first described as a species of *Ascarina* in Chloranthaceae (Schlechter 1906), and the genus *Idenburgia* (now in *Sphenostemon*) was described in Trimeniaceae (currently ANITA grade) by Gibbs (1917) (Figs. 1, 3). Both *Paracryphia* and *Sphenostemon* have some superficial resemblance to these basal angiosperms (see also Jérémie 1997, 2008). However, on closer inspection, especially when the internal floral morphology is studied, this resemblance quickly disappears. Cronquist (1981) placed *Paracryphia* as a separate family in Theales of Dilleniidae, and *Sphenostemon* in Aquifoliaceae of Rosidae. It appears that the high degree of synorganization of the floral organs, as characteristic for asterids, was lost to a considerable degree in Paracryphiaceae and Sphenostemonaceae; only syncarpy was retained (see also Endress 2002, 2008). The third family of Paracryphiales, Quintiniaceae, once in Saxifragaceae (see above, Engler 1930; not mentioned in Cronquist 1981), has retained somewhat more floral organ synorganization, and its floral structure appears very different from that of the other two families (Endress 2010a).

2. *Hydatellaceae* were originally placed in Centrolepidaceae, a family of Poales, in advanced monocots. That they did not fit in this family was first found in morphological and embryological studies by Hamann, who placed them in a separate family of unknown position in monocots (Hamann 1975, 1976). Hydatellaceae are wetland plants with extremely reduced flowers. Phylogenetic studies based on molecular and morphological features relegated the family to Nymphaeales of basal angiosperms (Saarela et al. 2007) (Fig. 1). Subsequently this was further supported by more detailed structural studies by, e.g., Rudall et al. (2007).

Floral features that are more labile than previously thought

Some features of floral architecture and organization apparently are evolutionarily flexible and are present in quite

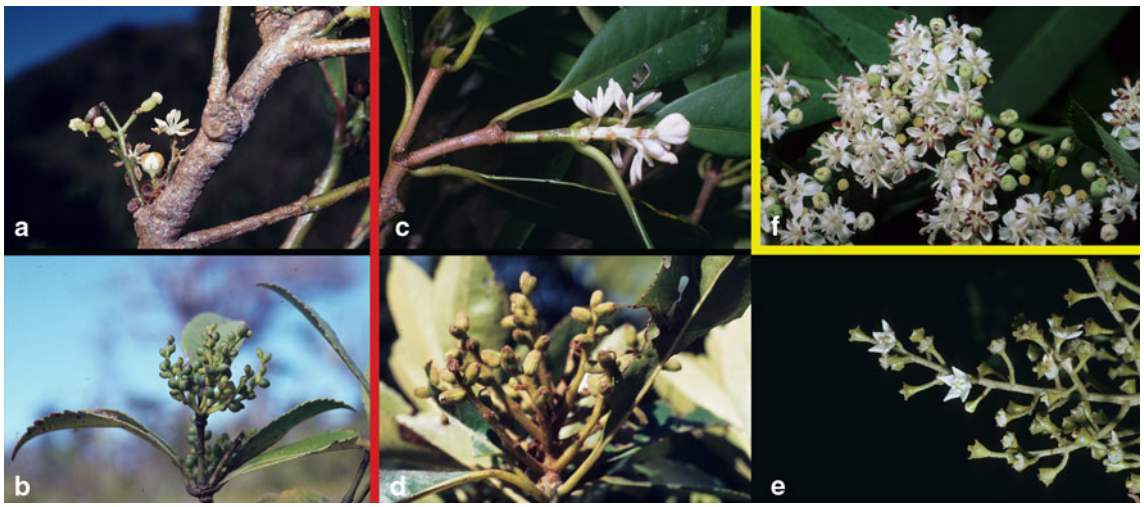

Fig. 3 Paracryphiales and their earlier putative relatives and current sister group. **a** *Trimenia neocaledonia* Baker f. (Trimeniaceae, Austrobaileyales, ANITA grade). **b** *Ascarina solmsiana* Schltr. (Chloranthaceae, Chloranthales, ANITA grade or sister to magnoliids). **c**-**e**. Paracryphiales (asterids). **c** *Sphenostemon lobosporus* (F. Muell.) L.S. Sm. (Sphenostemonaceae). **d** *Paracryphia alticola* (Schltr.) Steenis (Paracryphiaceae). **e** *Quintinia quatrefagesii* F. Muell. (Quintiniaceae). **f** *Sambucus ebulus* L. (Adoxaceae, Dipsacales, asterids). The *red* line separates the components of two pairs that were earlier regarded as closely related. The *yellow* line separates the three members of Paracryphiales from a member of its sister clade, Dipsacales

disparate clades as shown above in section "Former circumscriptions with considerable changes," such as flower size, floral phyllotaxis, floral symmetry, decrease and increase in floral organ number, loss of perianth, loss and reappearance of corolla, choripetaly/sympetaly, diplostemony/obdiplostemony, presence or absence of polystemony, centripetal/centrifugal stamen initiation in polystemonous androecia, features of a buzz pollination syndrome, and features used in alpha-taxonomy to describe gynoecia, e.g., inferior or superior ovaries. The current classifications (Stevens 2001 onwards; Soltis et al. 2005; APG 2009; Reveal 2011; Reveal and Chase 2011) indicate that these features are less suitable to characterize larger clades than previously thought. Some of these and other features and their lability are briefly discussed in this section.

Floral phyllotaxis: In basal angiosperms and basal eudicots there is much evolutionary plasticity between spiral and whorled floral phyllotaxis (Endress 1987; Endress and Doyle 2007, 2009). Optimization studies show at least eight changes in the perianth phyllotaxis and seven in the androecium phyllotaxis, and the most parsimonious ancestral state of floral phyllotaxis in angiosperms is equivocal (Endress and Doyle 2007; Doyle and Endress 2011). Especially labile are Atherospermataceae and Monimiaceae among magnoliids (Staedler and Endress 2009), and Ranunculaceae in basal eudicots (Schöffel 1932; Ren et al. 2010).

Presence/absence of perianth: In basal eudicots the perianth was lost several times, among Ranuncululales, in Eupteleaceae (Endress 1986; Ren et al. 2007) and *Achlys* (Berberidaceae, Endress 1989c), among Trochodendrales (almost) in *Trochodendron* (Endress 1986; Wu et al. 2007), among Buxales in *Styloceras* (von Balthazar and Endress 2002a, b) and *Didymeles* (von Balthazar et al. 2003), and among Gunnerales in certain Gunneraceae (Rutishauser et al. 2004; Ronse Decraene and Wanntorp 2006) and (probably) in Myrothamnaceae (Jäger-Zürn 1966).

Presence/absence of corolla: In basal eudicots (Endress 2010a), Caryophyllales (Brockington et al. 2009), and other core eudicots (Ronse Decraene 2008) petals disappeared and reappeared several times.

Choripetaly/sympetaly: There are instances of sympetaly in many mainly choripetalous clades (e.g., Schönenberger et al. 2005). Examples in basal eudicots are Papaveraceae (*Adlumia*) and Ranunculaceae (*Consolida*); in Saxifragales, sympetaly evolved multiple times in Eurasian Sedoideae (*Umbilicus*, *Sedum*, *Pistorinia*, *Sedum*, *Rosularia*, and *Prometheum*) ('t Hart et al. 1999) and probably also in other Crassulaceae; in Malpighiales, in Euphorbiaceae, in male flowers of *Crotonogyne*, *Manniophyton*, *Pausandra* (Pax and Hoffmann 1931), in Dichapetalaceae, in *Tapura*, petals and stamens are fused (Engler and Krause 1931; Matthews and Endress 2008); in Sapindales, in Meliaceae, in *Munronia*, *Turraeanthus*, species of *Turraea*, *Chisocheton*, *Dysoxylum*, *Aglaia*, and commonly fused with the staminal tube (Harms 1940; Mabberley 2011), and in Rutaceae, in the Angostura alliance (Galipeinae) (Engler 1931; Kubitzki et al. 2011); in Santalales, in Olacaceae (*Schoepfia*; Tomlinson 1980). It should be emphasized that in some of these cases it is not established whether there is true sympetaly, i.e., with congenital petal union, or only postgenital coherence of petals.

Vice versa, there are many instances of choripetaly in predominantly sympetalous clades. This is especially the case in Ericales; Cyrillaceae are choripetalous, perhaps primitively (?) (Anderberg and Zhang 2002), but secondarily according to Schönenberger et al. (2005); the clade of Sarraceniaceae, Actinidiaceae, and Roridulaceae is choripetalous (Schönenberger et al. 2005); in Clethraceae both choripetaly and sympetaly are present (Anderberg and Zhang 2002); the same in Marcgraviaceae (Schönenberger et al. 2005) and Actinidiaceae (Dickison 1972); within Ericaceae, Empetreae, most Monotropoideae, and scattered genera elsewhere (in Monotropoideae potentially primitively choripetalous) (Stevens et al. 2004). Similarly, Cornales are labile (Hufford 1992). In Lamiales, in Plantaginaceae the reduced flowers of *Besseya* are choripetalous (Hufford 1995). In Paracryphiales, flowers appear choripetalous, but development has not been studied (Endress 2010a). For the evolution of sympetaly and fluctuations between sympetaly and choripetaly in basal asterids, see also Endress (1997a) and Ronse Decraene et al. (2000).

Diplostemony/obdiplostemony: Diplostemony and obdiplostemony often occur in the same order or even family, which indicates that they are not fundamentally different (in contrast to some earlier beliefs of a different evolutionary derivation of the two, e.g., Corner 1946) (see also below under "Stamen initiation centripetal/centrifugal"). For instance, we found both patterns in Cucurbitales, Crossosomatales, and the Rhizophoraceae alliance, among those even in the same family and subfamily (Linaceae, Hugonioideae) (Matthews and Endress 2002, 2004, 2011). Which of the two patterns is realized during development depends on minute differences in the development of the two stamen whorls (see Rohweder 1963; Eckert 1966; Ronse Decraene and Smets 1995; Endress 2010b).

Oligostemony/polystemony: Coexistence of oligostemony (not more than two stamen whorls isomerous with perianth whorls) with polystemony was found in almost all orders studied in the rosid project by Matthews and Endress: Oxalidales (Cunoniaceae and Elaeocarpaceae; Matthews and Endress 2002), Cucurbitales (Datiscaceae and Begoniaceae; Matthews and Endress 2004), Crossosomatales (Crossosomataceae and Aphloiaceae; Matthews and Endress 2005b), especially prominent among Malpighiales (Wurdack and Davis 2009), in Chrysobalanaceae s.l. (Chrysobalanaceae, partly/slightly in Dichapetalaceae and Trigoniaceae; Matthews and Endress 2008), the Rhizophoraceae alliance (Rhizophoraceae and Caryocaraceae; Matthews and Endress 2011), also in the Euphorbiaceae alliance (Prenner et al. 2008) and the Clusiaceae alliance (Stevens 2007). This coexistence of oligo- and polystemony also occurs in Saxifragales (Hamamelidaceae, Endress 1989a; Paeoniaceae, Hiepko 1965), Fabales, Geraniales, Myrtales, and Sapindales in the rosid alliance and in the Fouquieriaceae–Polemoniaceae clade, the Hydrangeaceae–Loasaceae clade, and Araliaceae in asterids (Hufford 1990; Hufford et al. 2001; Endress 2002; Schönenberger and Grenhagen 2005; Schönenberger 2009; Nuraliev et al. 2010). The evolutionary pathway to polystemony among diplo- or haplostemonous groups appears to be commonly via double or multiple positions within distinct floral sectors, such as in all mentioned larger clades of rosids with some polystemony studied by us. With regard to the relation between polystemony and oligostemony, earlier works did not consider the hierarchy of the different systematic levels where they occur, but rather just made uniform statements lumping all levels together (e.g., Reuter 1926).

Stamen initiation centripetal/centrifugal: Corner (1946) studied the development in several centrifugal–polystemonous genera and regarded this pattern as "a feature of considerable systematic importance," which led to the creation of the subclass Dilleniidae (see above; Cronquist 1957; Leins 1975). However, the recognition of the multiple evolution of this trait by molecular phylogenetic studies later led to the dismantling of the subclass Dilleniidae (see above, "Former subclasses"). Corner (1946) also thought that obdiplostemonous groups "seem referable to the centripetal series." However, later it was clearly shown that obdiplostemonous flowers do not exhibit centrifugal stamen initiation (Rohweder 1963; Eckert 1966; Endress 2010b; Leins and Erbar 2010) and that there is lability between diplostemony and obdiplostemony.

Ovary superior/inferior: Evolutionary relationships between these two features and the occurrence of multiple evolutionary transitions from inferior to superior ovaries within families, e.g., in Rubiaceae and Araliaceae, were discussed in Endress (2011b).

Placentation axile/parietal: These features are likewise unstable and have evolved many times (Endress 1994a; Ronse Decraene 2010). The earlier order name Parietales for a group of 34 families (Engler 1925, based on Lindley) reflects the former systematic weight put on this kind of placentation. These families are now dispersed in 11 orders (Canellales, Dilleniales, Cucurbitales, Malpighiales, Oxalidales, Crossosomatales, Capparales, Malvales, Caryophyllales, Ericales, and Cornales), placed in magnoliids, rosids, and asterids.

Apocarpy/syncarpy: Earlier, apocarpy has been seen as primitive everywhere and syncarpy as derived. In a syncarpous gynoecium it is easy to develop a compitum, an area where pollen tubes are able to cross between carpels, which greatly increases pollen tube selection (Endress 1982). However, a compitum can also be reached by various means in an apocarpous gynoecium, especially by postgenital fusion of free carpels, and apocarpy evolved several times from syncarpy in eudicots and monocots

(Endress et al. 1983; Doyle and Endress 2000; Endress and Doyle 2009; Remizowa et al. 2010; Endress 2011c; Wang et al. 2012).

Features or combinations of features that are more stable than previously thought or have not been considered

Ovule structure in particular is more diverse than traditionally recognized, and patterns of this diversity are also of a certain stability and of macrosystematic interest. This was shown by a broad review of the floral morphological and embryological literature of angiosperms (Endress 2003, 2005, 2010a, 2011a, c) and also by our own comparative studies in basal angiosperms (summarized in Endress and Igersheim 2000) and a number of larger clades in core eudicots, especially rosids (Matthews et al. 2001; Matthews and Endress 2002; 2004, 2005a, b, 2006, 2008, 2011; Endress and Matthews 2006a, b). Through these studies, features were recognized in ovule structure that were not considered in previous embryological publications (Endress 2011a).

Nucellus thickness: it is useful not only to distinguish between crassinucellar and tenuinucellar, but also to distinguish between: (1) weakly crassinucellar (with only one cell layer between meiocyte and epidermis of the nucellus apex; e.g., in Zygophyllales of rosids), (2) pseudocrassinucellar (with no cell layer between meiocyte and epidermis of the nucellus apex, but periclinal division of epidermal cells; e.g., in some basal eudicots and some basal monocots), (3) incompletely tenuinucellar (with the meiocyte hypodermal in the nucellus apex but with hypodermal tissue at the flanks of the meiocyte and/or below the meiocyte in the nucellus; e.g., in many groups of the COM clade of rosids and in basal asterids), and (4) reduced tenuinucellar (with the meiocyte hypodermal throughout the nucellus and partly extending below the nucellus; e.g., in many Gentianales) when describing ovules (Endress 2003, 2005, 2010a, 2011a, b).

Endothelium: An endothelium is mostly associated with tenuinucellate ovules. However, there are also cases of tenuinucellar ovules *without* an endothelium (Gentianales) and, vice versa, cases of incompletely tenuinucellar, weakly crassinucellar, or even crassinucellar ovules *with* an endothelium (Malpighiales and Cornales).

Integument number: Ovules with two integuments characterize basal angiosperms, monocots, basal eudicots, rosids, Caryophyllales of the asterid alliance, and a few basal asterids. Ovules with one integument are present in almost all asterids. A number of groups transferred from rosids or other core eudicots to asterids based on molecular analyses have only one integument (e.g., Loasaceae, Hydrangeaceae, Cornaceae, and Eucommiaceae). Thus, in the current classification, integument number is an even stronger marker than it was in the precladistic era (see also Endress et al. 2000).

Integument thickness: The outer integument is commonly thicker than the inner or equally thick (in the latter case often both with only two cell layers). However, ovules with the inner integument thicker than the outer characterize many malvids and many groups of the COM clade (Endress and Matthews 2006b).

In addition to stable features it is also of interest to consider unique combinations of features. This is especially useful in the study of floral fossils. An example are Hamamelidaceae by their unique combination of laterally hinged anther valves, basifixed anthers, connective appendage, and bicarpellate gynoecium, features easily recognizable in fossils (Endress 1989a, b; Hufford and Endress 1989; Endress and Friis 1991; Magallón-Puebla et al. 1996; Magallón et al. 2001; Magallón 2007). The combination of laterally hinged anther valves, basifixed anthers, and connective appendage is also common in Magnoliales, but they have a different gynoecium structure (Endress and Hufford 1989; Endress 1994b).

New features of macrosystematic interest or features to be further explored

The following features were more recently shown to be of considerable macrosystematic interest in our studies and in those of other laboratories. Most of them cannot be recognized without microtome sections, and therefore they were often missed or neglected in previous literature. They should however be followed up more closely in future studies.

Special mucilage cells in sepals with a thickened inner cell wall are common in many rosids, particularly fabids, but absent or rare in other eudicots and basal angiosperms (Matthews and Endress 2006).

Petals (and not sepals) covering inner floral organs in advanced bud, often combined with valvate aestivation and incurved tip, is a combination more common in core eudicots than earlier considered, for instance, in Vitales, among Malpighiales, in Dichapetalaceae (Matthews and Endress 2008) and some Rhizophoraceae and Erythroxylaceae (Matthews and Endress 2011), among Sapindales, especially in Burseraceae and Spondiadoideae of Anacardiaceae (Bachelier and Endress 2009), among the asterid alliance, in Santalales, (Endress 2008; Wanntorp and Ronse De Craene 2009), Cornales, and in campanulids (Endress 2010a). Thus, the distinction between sepals and petals based on three versus one vascular trace and the protective versus nonprotective function combined with

early growth versus delay in growth (e.g., Endress 1994a) is often not present.

In flowers with united petals, union may be congenital or postgenital or both combined. These patterns should be more closely studied and distinguished. The term "sympetaly" should only be used for corollas with congenitally united petals. This is the most common pattern of petal union. Postgenitally united petals occur, e.g., in a few Oxalidales (Matthews and Endress 2002), Celastrales (Matthews and Endress 2005a), and Malpighiales (Matthews and Endress 2011). The combination of congenital and postgenital union is known from some Gentianales (Endress 2010a).

In sympetalous flowers, late and early sympetaly may be distinguished (Erbar and Leins 1996, 2011). Late sympetaly, in which the individual petal primordia are distinct from the beginning of corolla development, largely characterizes lamiids, whereas early sympetaly, in which the individual petal primordia become distinct only after the beginning of corolla development, primarily occurs in campanulids (Erbar and Leins 1996, 2011).

Stapet, the congenital fusion of stamens with petals (Ritterbusch 1991), evolved in many monocots and eudicots. In core eudicots it is often combined with sympetaly; thus, it is especially common in asterids. In rosids, sympetaly with stapet is unusual but is more common than it may appear from general descriptions. Examples are in Rutaceae (part of the Angostura alliance = Galipeinae, Sapindales; Kubitzki et al. 2011), Caricaceae (Brassicales; Ronse Decraene and Smets (1999b), and in Crassulaceae (Saxifragales; Wassmer 1955). In basal eudicots it is present without sympetaly, e.g., in Berberidaceae and Sabiaceae. While in euasterids sympetaly is ubiquitous and a stapet is most common, in basal asterids choripetaly occurs in addition to sympetaly, and a stapet is present or absent in sympetalous taxa.

Differential length of stamens in flowers with two stamen whorls. In many (ob)diplostemonous core eudicots the antepetalous stamens are smaller (shorter) than the antesepalous ones, or they have the same size. Only rarely are the antepetalous stamens larger than the antesepalous ones, e.g., in a number of taxa of the Rhizophoraceae alliance, such as in many Rhizophoraceae, in Erythroxylaceae, and in *Hugonia* (Linaceae) (Matthews and Endress 2011). Both the general basis for the mostly smaller antepetalous stamens and the systematic distribution of the different morphs should be studied in more detail.

Different developmental patterns of polystemony: Since polystemony and both centripetal and centrifugal initiation of polystemony have evolved in many clades of (core) eudicots as mentioned above, it may be useful to look for subpatterns within these broad developmental patterns. This has been done for some clades, but much more comparative research is necessary to determine whether there are subpatterns of special systematic distribution. The most extreme configuration is ring primordia with centrifugal stamen initiation known from Dilleniaceae (*Dillenia*, *Tetracera*; Corner 1946; Ronse Decraene and Smets 1992; Endress 1997b), Salicaceae (Bernhard and Endress 1999), Capparaceae (*Capparis*, Leins and Metzenauer 1979), Malvaceae (*Adansonia*; van Heel 1966; Janka et al. 2008), Aizoaceae (*Aptenia*, Aizoaceae; Ronse Decraene and Smets 1992; Cactaceae several genera, Ross 1982; *Pereskia*, Leins and Schwitalla 1985; *Opuntia*, Ronse Decraene and Smets 1992), Theaceae-Camellioideae (*Polyspora*, *Camellia*, *Pyrenaria*; Tsou 1998), and Lecythidaceae (Tsou and Mori 2007). Thus the pattern is present especially in malvids, including the COM clade and in basal groups of the asterid alliance (Endress 2010a). Ring primordia with centripetal stamen initiation occur in basal eudicots (Papaveraceae, Nelumbonaceae; Merxmüller and Leins 1967; Karrer 1991; Ronse Decraene and Smets 1993; Hayes et al. 2000) and a few rosids (Ronse Decraene and Smets 1991). Ring primordia with bidirectional or almost simultaneous stamen initiation characterize Achariaceae (Bernhard and Endress 1999; Endress 2006). Other patterns of polystemony, which do not operate with ring meristems, for instance, sectorial primary meristems (e.g., in malvids, von Balthazar et al. 2006), are less well characterized and need more comparative studies. Some patterns appear disparate within a group at first sight, but a common pattern may be found when the entire diversity is studied in more detail (e.g., Loasaceae, Hufford 1990). To speak of centrifugal patterns only makes sense if all organs or modules compared in a system are equally developed and not partly reduced (not considered in Rudall 2010). In many cases reduced organs appear later in development than their well-developed counterparts (Endress 2008). However, whether they are really later initiated or just early inhibited after initiation has in most cases not been critically studied.

A *basal androecial tube (by congenital union) with nectary on outside or inside* is present in some Malpighiales: Rhizophoraceae alliance (all families except Irvingiaceae) (Matthews and Endress 2011), and Ixonanthaceae (Link 1992); Oxalidales: Oxalidaceae, Connaraceae (Matthews and Endress 2002); Celastrales: Lepidobotryaceae (Matthews and Endress 2005a); Geraniales: Geraniaceae, partly Melianthaceae (Ronse Decraene et al. 2001; Endress 2010b).

An *androgynophore or gynophore* (mostly only short) occurs in Oxalidales (Matthews and Endress 2002) and some Celastraceae (Matthews and Endress 2005a) and Malpighiales (Endress and Matthews 2006b; Matthews and Endress 2011). It is also present in a number of malvids (often more prominent), such as Brassicales, Malvales, Sapindales, and Crossosomatales (Matthews and Endress

2005b; Endress and Matthews 2006b; Bachelier and Endress 2009).

Angiospermy type 4 (angiospermy by complete postgenital fusion, as defined in Endress and Igersheim 2000) is the most common type in the six larger rosid clades studied (Oxalidales, Cucurbitales, Celastrales, Crossosomatales, Chrysobalanaceae s.l. of Malpighiales, and Rhizophoraceae alliance of Malpighiales), but in all clades (except Celastrales), also type 3 (angiospermy by a partial secretory canal and complete postgenital fusion at the periphery) and rarely type 2 (angiospermy by a continuous secretory canal and partial postgenital fusion at the periphery) occur (Matthews and Endress 2002, 2004, 2005a, b, 2008, 2011).

The gynoecium is *at least partly (syn)ascidiate* in most taxa of the mentioned six larger rosid clades. There are only very few exceptions with the gynoecium completely (sym)plicate (e.g., Cephalotaceae of Oxalidales, Matthews and Endress 2002; Datiscaceae and some Cucurbitaceae in Cucurbitales, Matthews and Endress 2004); the proportion of the symplicate and synascidate zones often varies at relatively low systematic levels.

A normal intracarpellary *compitum* appears to be present in all six mentioned larger rosid clades (the few apocarpous or nearly apocarpous taxa among them need further study); however, an apical compitum by postgenital fusion of the initially free carpel tips occurs in at least two of the six larger clades (several Crossosomatales; Matthews and Endress 2005b; *Trigoniastrum* of Chrysobalanaceae s.l.; Matthews and Endress 2008; probably at least in part together with a normal compitum in the symplicate zone).

Commissural (and not carinal) stigmas associated with strong commissural vascular bundles are characteristic for Celastrales (not in Lepidobotryaceae) (Matthews and Endress 2005a). They are otherwise not common but also occur in families of core Brassicales (e.g., Brückner 2000, not mentioned in Ronse Decraene and Haston 2006), in some Myrtales (Onagraceae, Mayr 1969; Penaeaceae, Schönenberger and Conti 2003), and in derived taxa within Papaveraceae (Karrer 1991; Brückner 2000). In all these cases the carpels are congenitally united up to the stigmas.

A *ventral furrow tapering downward as an external furrow in the ascidiate zone of the carpels* is characteristic in Oxalidales and Celastrales (Matthews and Endress 2002, 2005a).

The ovaries are dorsally bulged upwards in in some representatives of four of the six mentioned larger rosid clades (Celastrales, Cucurbitales, Chrysobalanaceae s.l., and Rhizophoraceae alliance) (Matthews and Endress 2004, 2005a, 2008, 2011). In addition, an *apical septum* (a structure originally described in Hartl 1962) was found in Celastrales and some families of the Rhizophoraceae alliance (Matthews and Endress 2005a, 2011). The presence of an apical septum is best known from a number of asterid families and Myrtaceae (Hartl 1962), and it is more common than originally thought (see also Endress 2011c).

Unifacial styles or tips of separate carpels (lacking a ventral slit) are characteristic for a number of Cucurbitales and Fagales (Baum-Leinfellner 1953; Endress 1967, 2008; Matthews and Endress 2004), and among Malpighiales for several families of the Rhizophoraceae alliance (Baum-Leinfellner 1953; Matthews and Endress 2011) and Passifloraceae (Baum-Leinfellner 1953; Bernhard 1999).

Antitropous ovules, often in combination with an obturator, occur in many Oxalidales, Celastrales, and Malpighiales (Matthews and Endress 2002, 2005a, 2008, 2011; Merino Suter et al. 2006) and thus are characteristic for the COM clade (Endress and Matthews 2006b). In addition, they are also known from some Sapindales (Bachelier and Endress 2008, 2009) and a few Crossosomatales (Matthews and Endress 2005b).

Unlike in many other rosids *the ovules are not crassinucellar, but weakly crassinucellar or incompletely tenuinucellar and have an endothelium* in many representatives of the COM clade, i.e., Celastrales, Oxalidales, and Malpighiales (Matthews and Endress 2002, 2005a, 2008, 2011; Endress and Matthews 2006b; Endress 2011a). Likewise *the inner integument is mostly thicker* than the outer in a number of groups of the COM clade and of malvids (Endress and Matthews 2006b).

Conclusions

There are many more instances of "Brownian motion"-type evolution than earlier assumed, i.e., evolutionary fluctuations forwards and backwards in floral morphology and other features without a recognizable pattern or favored direction (Endress 1994a, p. 401; Losos 2011), yet this kind of evolution has been neglected in earlier macrosystematic discussions. In some instances it may in fact be so overwhelming that it will not be possible to track evolutionary changes in detail (Losos 2011). Thus, we need to become accustomed to the fact that it may become more and more difficult to use the term "synapomorphy" for features of larger clades. Instead, we need to substitute it nolens volens by "tendencies" or "trends." The way features evolve is much more complex (and flexible) than previously thought. For recent discussions on parallelism and homoplasy, see also Ronse Decraene (2010), Scotland (2011), and Wake et al. (2011).

In some cases, more refined study of these features may reveal more stable features; for instance, in the crude distinction between centrifugal and centripetal stamen initiation in polystemonous androecia, subpatterns may occur, as shown above.

The same feature may be stable in one group but labile in another (independent of the systematic hierarchy). This is nothing new but needs to be constantly emphasized.

Features (and floral architectures, i.e., suites of features) tend to evolve repeatedly in very different clades, but more often in closely related groups than in distant groups.

The way features evolve is more complex and dynamic than previously thought. The more it becomes possible to track fine-grained evolutionary changes of features based on ever more refined phylogenetic analyses, the more it becomes clear that within a family or genus a feature may have evolved many times. A good example for such a complex evolutionary situation is floral symmetry in Old World Malpighiaceae (Davis and Anderson 2010). This does not mean that we step back to an earlier stage of knowledge. On the contrary, we know much more about evolution, and we should now actively concentrate on the detailed mechanisms of the evolution of prominent floral features.

Thus, more detailed focus on the mechanisms by which prominent features evolve becomes necessary. For this, we also need to learn in more detail not only whether features are present or absent within a group, but also how they are distributed within the group: either more randomly (as in the mentioned Brownian motion pattern) or concentrated in certain subclades (by differential canalization of evolutionary trends), e.g., more in derived subclades than in basal subclades of a larger clade. Better knowledge of their significance in a biological context is also important (see also Endress 2003, 2011b). This is a continuing challenge.

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